

A NEW HYBRID CHERRY, *PRUNUS* × *PUGETENSIS* (*P. AVIUM* × *EMARGINATA*, ROSACEAE), FROM THE PACIFIC NORTHWEST

ARTHUR L. JACOBSON

2215 E. Howe St., Seattle, WA 98112

PETER F. ZIKA¹

Herbarium, Box 355325, University of Washington, Seattle, WA 98195-5325

ABSTRACT

A natural hybrid, *Prunus* × *pugetensis* A. L. Jacobson & Zika, is described as the cross between introduced *Prunus avium* (L.) L. of Eurasia, and indigenous *P. emarginata* (Douglas ex Hook.) Eaton of western North America. It is intermediate in morphology, differing from *P. avium* in its pubescence, more slender leaves, smaller flowers, and peduncled inflorescences. It can be separated from *P. emarginata* by its broader leaves with coarser teeth, larger flowers with weakly notched petals, and occasional umbellate inflorescences. Unlike the parents, more than 99% of the flowers eventually abort and it rarely produces fruit. Spontaneous hybrids have been found in the lowlands of western British Columbia, Washington, and Oregon.

Lectotypes are selected for *Cerasus californica* Greene, *Cerasus emarginata* Douglas ex Hook., *Cerasus erecta* C. Presl, *Cerasus kelloggiana* Greene, *Cerasus mollis* Douglas ex Hook., and *Prunus corymbulosa* Rydb.

Key Words: hybrid, lectotype, *Prunus avium*, *Prunus* × *pugetensis*, *Prunus emarginata*, Puget Sound, Rosaceae.

Prunus is a highly varied genus of widely distributed trees and shrubs, united by floral and fruit characters, and a base chromosome number of $x = 8$ (Bortiri et al. 2001). Estimates of the number of species of *Prunus* sensu lato range from 200+ (Mabberley 1997) to 430 (Huxley et al. 1992). As we view it, the genus consists of almonds, apricots, cherries, peaches, plums, and cherry laurels. Some botanists (e.g., Browicz and Zohary 1996; Lu et al. 2003) divide *Prunus* sensu lato into as many as six genera, restricting the genus *Prunus* exclusively to plums (Endo 2001; Ku and Bartholomew 2003a). In that sense, the cherries become *Cerasus* Mill., *Padus* Mill., and *Laurocerasus* Duhamel (Ohba and Endo 2001; Li and Bartholomew 2003; Ku and Bartholomew 2003b; Lu and Bartholomew 2003). Our view, like that of the majority of taxonomists in North America, is to consider *Prunus* in the broad sense, including *Cerasus* and the other groups as subgenera and sections (Rehder 1940; McVaugh 1951; Mowrey and Werner 1990). This view is supported by the molecular work and conclusions of Lee and Wen (2001), Bortiri et al. (2001), and Rohrer et al. (2004).

Washington state is a major source for commercial sweet cherries, and has plentiful native cherries. In the late 1980s the first author noticed cherry trees whose identification perplexed him. Since the late 1990s we analyzed these wild cherries, and they appeared intermediate between native *Prunus*

emarginata (Douglas ex Hook.) Eaton and the widely cultivated and naturalized *P. avium* (L.) L. Careful appraisal of our data suggests they represent a hybrid. The trees are intermediate in morphology; we have done no cytological or molecular analysis. In this paper we provide descriptions, a key, and comparative tables for the hybrid and its parents. We also reviewed the synonyms of *P. emarginata* and inspected all available types to be sure none represented the hybrid between *P. avium* and *P. emarginata*. We found six epithets typified by a series of syntypes and no holotype, so in this paper we designated a lectotype, based on the protologues and the best of the original material available to the authors when the basionym was published, in accordance with the Code (Greuter et al. 2000).

SPECIES TREATMENT

Prunus × *pugetensis* A. L. Jacobson & Zika
hyb. nov. (*Prunus avium* × *P. emarginata*).
(Fig. 1).—TYPE: USA, Washington, Snohomish Co., wooded slope 0.3 km W of Blackmans Lake; below SW side of Bickford Ave, 50 m S of Rte 9 bridge, elev. 60 m, 47°55.9'N, 122°6'W, 4 May 2003, Zika 18302. (Holotype: WTU; isotypes: CAN, GH, K, MO, NY, OSC, RM, RSA, UBC, UC, US, V, WS).

Arbor inter *Prunus avium* et *Prunus emarginata* verosimiliter ex hybridatione specierum orta, ambae fructibus abortivis differt; differt a *P. avio* foliis angustioribus et pubescentibus cum dentibus minoribus et plus numerosis, petalis

¹ Author for correspondence, email: Zikap@comcast.net

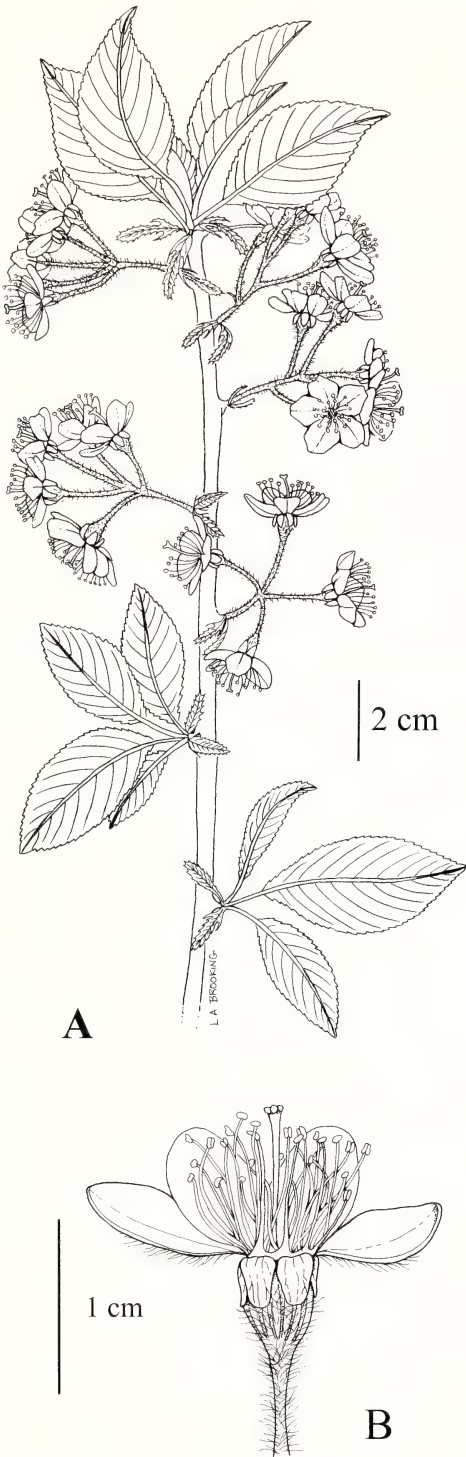


FIG. 1. *Prunus* $\times$ *pugetensis*. A) Habit (Zika 18303). B) Flower with one petal removed.

pubescentibus et minoribus, ramunculis pubescentibus, inflorescentiis variantibus ex umbellatis ad pedunculatis vel corymbosis; differt a *P. emarginata* foliis obovatis longioribus dentatis, petalis 7–14 mm.

Tree, attaining 27 m in height and 48 cm diameter at breast height in the forest, flowering at 3–5 m; solitary or spreading by root sprouts; bark usually dark gray to dark coppery-brown, somewhat shiny and smooth, with pale thin corky horizontal lenticles; twigs brown, slender, new growth pubescent (rarely glabrous Zika 19380); winter buds narrowly ovate, several red-brown to dark red-brown scales, proximal scales slightly ciliate-serrate near apex; leaf scar crescent-shaped to triangular, with a central elliptical to circular bundle scar, this larger than the two lateral circular bundle scars near distal or lateral margin of leaf scar; leaves folded in bud (conduplicate), alternate, thin, elliptic-obovate or narrowly obovate, 4.4–14.7 $\times$ 2.1–5.8 cm wide in mid-summer; usually pubescent, mid-green, paler below, serrate, 6–11 teeth per cm in mid-summer, teeth 0.1–1.1 mm high measured from sinus; petiole apex often with 1–2 discoid glands 0.6–1.5 mm diameter; stipules 4–8 mm long, early deciduous, linear to narrowly lanceolate, pectinate to deeply lacerate; leaves deciduous in late October, when turning soft pastel shades of yellow, orange, reddish, or occasionally purple; inflorescence axillary, variable, an umbel, peduncled umbel, or corymb, 2–9 flowers per inflorescence, pubescent; rachis 0–1.4 cm; peduncle 0–31 mm long; peduncle uncommonly bearing 1–2 leafy bracts 10–26 $\times$ 4–10 mm wide, bracts crenate or serrate with shallow teeth 0.4–0.5 mm high; flowers white, rotate, 13–28 mm diameter (fresh), hypanthium campanulate, pubescent, petals 5, suborbicular or squarish, varying to ovate, elliptic, or broadly elliptic-oblong, 6.8–14 mm long, entire to slightly notched, base glabrous to lightly pubescent with long crinkled hairs on inner surface, outer surface thinly hairy; sepals green, entire, reflexed in flower, 2.4–3.2 mm long, margins ciliate or glabrous, outer surface glabrous (Zika 19380) or more commonly lightly pubescent, broadest at base, lance-oblong; stamens 20–38; anthers yellow, broadly elliptic, 0.5 mm long (dried); filaments white, filiform, 3–10 mm long, inserted in 2–3 loose series at or near apex of hypanthium, ovary glabrous, ovate, 2 ovules (only one maturing), stigma a flattened irregular disk 0.6–0.7 mm wide; style filiform, 0.8–0.9 mm long, slightly broadened at base and at apex; most ovaries aborting; pedicel in flower 5–35 mm long, pubescent and often glandular, often subtended by slender quickly deciduous stipule-like pale bracts; fruiting receptacle a disk 1.5–2.2 mm wide; fruit subglobose to broadly elliptic-globose, recessed at pedicel attachment; green when immature, ripening to yellow, brownish yellow, or red, with yellow to red blush, with a darker longitudinal line on one side, fruit 10–17 $\times$ 9–19 mm wide, slightly shiny, glabrous, flesh 3–4 mm thick, juicy, slightly bitter and slightly sour; seed elliptic-globose, slightly flattened, pale

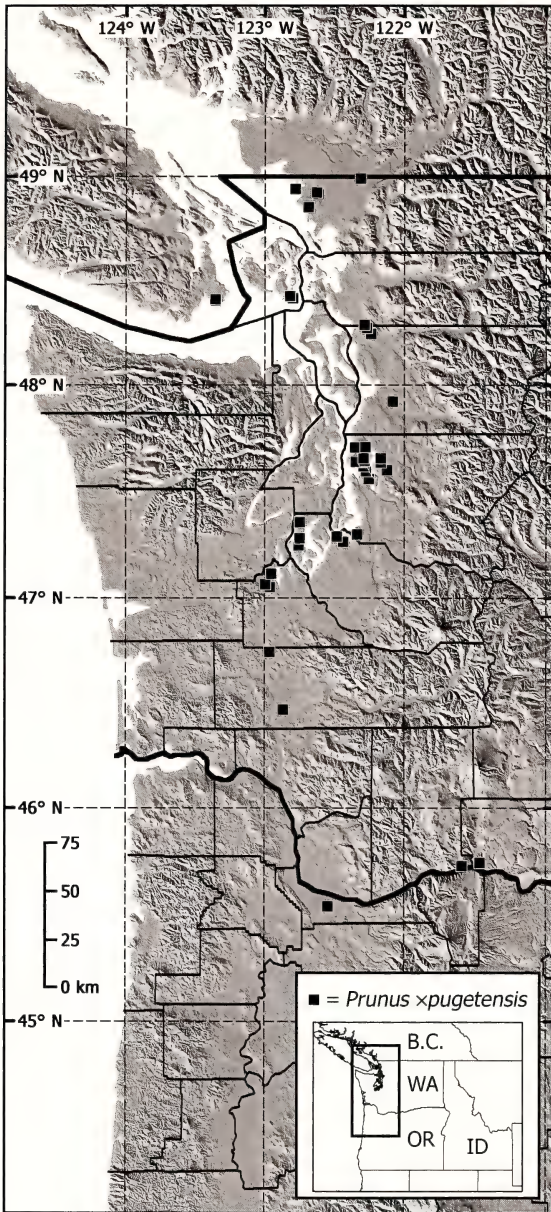


FIG. 2. Distribution of *Prunus xpugetensis*.

brown, 7–11.1 × 5.0–7.8 mm wide, with 5 strong grouped and raised longitudinal ridges, as well as 2–4 small straight unbranched lateral raised veins. Chromosome number unknown.

Distribution. Known populations of the hybrid extend from Portland, Oregon, north to Victoria, Vancouver Island, in southwestern British Columbia, and include the islands of northern Puget Sound (Fig. 2). All known populations are from low elevations west of the Cascade Mountains, and in the Columbia River Gorge. This is entirely within the overlap of native populations of *Prunus emarginata* and naturalized *P. avium*. To

commemorate the type locality and its presently known center of distribution, we propose an epithet for Puget Sound.

Paratypes. CANADA, BRITISH COLUMBIA: Vancouver Is., Victoria, Beacon Hill, E slope near summit, elev. 40 m, 6 May 2002; *Zika 16848 et al.* (UVIC, V, UBC, DAO, CAN, TRT, WTU); Vancouver Is., Victoria, Beacon Hill, near Michigan Street, elev. 15 m, 6 May 2002, *Zika 16846 et al.* (UC, K, NY, MT, CAN, DAO, UBC, V, OVIC, UWO).

USA, OREGON: Multnomah Co., Portland, junction of Routes I-84 and I-205, elev. 100 m, 12 Apr 2004, *Zika 19358* (OSC, WTU).

WASHINGTON: King Co., Seattle, Montlake, near SW shore of Portage Bay, elev. 15 m, 20 Jun 2001, *Zika 16311 & Jacobson* (WTU); King Co., Seattle, Montlake, near Oceanography complex, elev. 20 m, 23 Apr 2004, *Zika 19412* (RSA, WTU); King Co., Seattle, Columbia, junction of S Oregon Street and 50th Avenue S, elev. 15 m, 13 May 2005, *Jacobson & Zika 20552* (WTU); King Co., Seattle, Queen Anne, Mt. Pleasant Cemetery, elev. 90 m, 13 May 2005, *Jacobson & Zika 20551* (WTU); King Co., Seattle, Carkeek Park, N of Pipers Creek, elev. 45 m, 13 May 2005, *Jacobson & Zika 20550* (WTU); King Co., Seattle, Capitol Hill, E Mercer Street, elev. 115 m, 20 Apr 2001, *Zika 15950 & Jacobson* (WTU); King Co., Seattle, Leschi, Mt. Baker Ridge, Frink Park, elev. 30 m, 20 Apr 2001, *Zika 15951 & Jacobson* (WTU); King Co., Seattle, Lake City, Thornton Creek floodplain, elev. 35 m, 21 May 2002, *Zika 16910 et al.* (WTU); King Co., Seattle, campus of University of Washington, near 45th Street, elev. 75 m, 26 Oct 2002, *Zika 18141 & Jacobson* (WTU); King Co., Bellevue, W shore of Larsen Lake, elev. 80 m, 20 Apr 2001, *Zika 15946 & Jacobson* (WTU); King Co., Bellevue, Route I-405, 11 May 2003, *Zika 18333* (K, PRA, WTU); King Co., Kirkland, Route I-405, 11 May 2003, *Zika 18334* (WTU); King Co., Redmond, SW side of Grass Lawn Park, elev. 95 m, 17 May 2006, *Zika 22736* GH; King Co., Federal Way, Saghale Playfield, elev. 100 m, 14 May 2002, *Zika 16869* (CAN, GH, K, MO, NY, UC, US); Klickitat Co., White Salmon, 3 air km S of McCoy Flat, elev. 260 m, 13 Apr 2004, *Zika 19380* (OSC, UC, WTU); Lewis Co., Centralia, Fords Prairie, Route I-5, elev. 60 m, 5 May 2003, *Zika 18308* (WTU); Lewis Co., Drews Prairie, Camas Road, elev. 100 m, 5 May 2003, *Zika 18310* (WTU); Pierce Co., 1.6 km N of Vaughn, Lacey Road, elev. 35 m, 5 May 2003, *Zika 18307* (WTU); Pierce Co., Key Peninsula, 1 km SE of Jackson Lake, elev. 85 m, 5 May 2003, *Zika 18303* (WTU); Pierce Co., Key Peninsula, 1 km W of Bay Lake, elev. 65 m, 5 May 2003, *Zika 18304* WTU; Pierce Co., Tacoma, corner of Tacoma Avenue and N 3rd

Street, elev. 80 m, 28 Apr 2002, *Zika 16819* (WTU); Pierce Co., Tacoma, 45th Street near Verde Street, elev. 80 m, 8 May 2002, *Zika 16851* (OSC, WWB); San Juan Co., Puget Sound, Lopez Is., Point Colville, elev. 15 m, 19 Apr 1996, *Naas 5746 & Arnot* (WTU); San Juan Co., Lopez Is., Watmough Head Road, elev. 30 m, 12 May 2003, *Zika 18341* (CAN, DAO, OSC, UBC, UC, V, WS); Skagit Co., 0.4 air km W of Interstate 5 on Route 20, elev. 10 m, 28 Apr 2006, *Legler 3307* (OSC, WTU); Skagit Co., Padilla Bay National Estuarine Research Reserve, near Interpretive Center, elev. 20 m, 5 May 2006, *Giblin 355* (OSC, WTU); Skamania Co., 3 air km SW of Underwood Mountain, elev. 410 m, 13 Apr 2004, *Zika 19376* (UBC, WS); Snohomish Co., 6 air km SW of Lake McMurray, elev. 95 m, 16 May 2002, *Zika 16877* (GH, MO, NY, OSC, UC, WS); Snohomish Co., 4.5 air km WSW of Lake McMurray, elev. 90 m, 16 May 2002, *Zika 16878* (CAN, DAO, MO, OSC, UBC, V); Snohomish Co., 2.5 air km N of Sunday Lake, elev. 105 m, 16 May 2002, *Zika 16882* (CAS, RSA, UC, WS); Thurston Co., Frye Cove County Park, 3 May 2000, *Wallding 29* ("evsc"); Thurston Co., Brenner Road near Simmons Road, elev. 10 m, 21 Apr 2004, *Zika 19404* (WTU); Thurston Co., 1.5 air km SW of Grass Lake, elev. 20 m, 21 Apr 2004, *Zika 19403* (DAO, RSA); Whatcom Co., 2.3 air km SW of Blaine, 28 Apr 2004, *Legler 1476* (OSC, WTU); Whatcom Co., SW shore of Lake Terrill, elev. 75 m, 28 Apr 2004, *Legler 1478* (WTU); Whatcom Co., 6 km W of Willey Lake, elev. 20 m, 24 May 2002, *Zika 16916* (GH, K, MICH, NY, OSC, RM, US, V, WS); Whatcom Co., 7 km E of Birch Bay, elev. 30 m, 24 May 2002, *Zika 16922* (CAS, ID, MO, MONTU, NY, PRA, RSA, SD, TRT, UWO); Whatcom Co., Halverstick Road, elev. 40 m, 26 Apr 2004, *Zika 19437* (WTU).

PARENTAGE

Prunus avium (L.) L., *Flora Suecica*, edition 2. 165. 1755.—*Prunus cerasus* L. var. *avium* L., *Species Plantarum* 1: 474. 1753. TYPE: 22 *avium* A (holotype: LINN, see Savage 1945).—*Cerasus avium* (L.) Moench, *Methodus Plantas Horti Botanici et Agri Marburgensis* 672. 1794. 2n = 16, 24, or 32 (Fogle 1975; Montgomery et al. 1997).

Prunus avium is common and fully naturalized in North America, wild in at least 30 states and five Canadian Provinces (Kartesz 2003), where it has been cultivated since about 1600. Its seedlings are a frequent rootstock used for grafting of various fruiting and flowering cherry trees; it rarely sends up root suckers except in woodland settings. Sweet cherry, or mazzard, is also grown purely as an ornamental tree.

In western Washington the flowers first appear in mid-March to April, well before *P. emarginata*, but the flowering period is long and the two overlap. The fruit ripens in early summer, at maturity variously red, purple, inky black, or rarely yellow, a color more typical of some cultivars. Yellow fruits are found in some hybrids, and never in *P. emarginata*. Autumn leaf color for *P. avium* is usually yellow (like *P. emarginata*), but can be a rainbow of green, yellow, orange and red, the same colors that can appear in the hybrid.

Prunus avium is immensely stronger, larger, and longer lived than *P. emarginata* and every other related species cultivated here except *P. serotina* Ehrh. It thrives both in the open and in forests. Woodland specimens can surpass 30 m tall; a stout open-grown tree can reach 17 m tall, its trunk 1 m in diameter, its crown 18.5 m across.

Prunus emarginata (Douglas ex Hook.) Eaton, *Manual of Botany for North America*, seventh edition. 463. 1836.—*Cerasus emarginata* Douglas ex Hook., *Flora Boreali-Americana* 1: 169. 1832. TYPE: USA, [Washington, Skamania Co.], common on the outskirts of woods near the Grand Rapids, [Columbia River, elev. 25 m, 45°40'N, 121°54'W; between 31 May and 3 June 1825], *D. Douglas s.n.* (lectotype, here designated, K-351910!).—*Prunus emarginata* (Douglas ex Hook.) D. Dietr., *Synopsis Plantarum* 3: 42. 1842.—*Prunus emarginata* (Douglas ex Hook.) Walp., *Repertorium Botanices Systematicae* 2: 9. 1843.

Cerasus mollis Douglas ex Hook., *Flora Boreali-Americana* 1: 169. 1832. TYPE: On the sub-alpine hills near the sources of the Columbia [River] and at its confluence [between 1825–1827], *D. Douglas s.n.* (lectotype, here designated, K-351908!), three twigs on the left side of the mixed sheet).—*Prunus mollis* (Douglas ex Hook.) Eaton, *Manual of Botany for North America*, Seventh Edition: 463. 1836. (Not *Prunus mollis* Torr., *Flora of the Northern and Middle Sections of the United States* 1: 470. 1824).—*Prunus mollis* (Douglas ex Hook.) Walp., *Repertorium Botanices Systematicae* 2: 9. 1843.—*Prunus emarginata* (Douglas ex Hook.) Eaton var. *mollis* (Douglas ex Hook.) Brewer, *Geological Survey of California, Botany* 1: 167. 1876.—*Prunus emarginata* (Douglas ex Hook.) Eaton var. *villosa* Sudw., *United States Department of Agriculture Division of Forestry Bulletin* 14: 240. 1897.—*Prunus pensylvanica* L. f. var. *mollis* (Douglas ex Hook.) B. Boivin, *Le Naturaliste Canadien* 93: 435. 1966.—*Prunus emarginata* (Douglas ex Hook.) Eaton subsp. *mollis* E. Murray, *Kalmia* 12: 23. 1982. *Cerasus erecta* C. Presl, *Epimeliae Botanicae* 194. 1851. TYPE: [Canada, British Columbia,

- northwest Vancouver Island] Nutkta Sund [Nootka Sound, 49°36'N, 126°34'W, in 1791], *T. P. X. Haenke s.n.* (lectotype, here designated, PRC!; isolectotypes: PR-612443!, PR-612444!). [The lectotype labels all mention "Mulgrav portum" (USA, Alaska, Yakutat, Port Mulgrave, 59°34'N, 139°47'W), but this is presumably an error for Haenke's Nootka gathering, on labels made after Haenke's death (Skocdoplová and Štěpánek 2002); the species is not otherwise reported from Alaska (Hultén 1968; Viereck and Little 1972).]—*Prunus erecta* (C. Presl) Walp., *Annales Botanices Systematicae* 3: 854. 1852.—*Prunus emarginata* (Douglas ex Hook.) Eaton subsp. *erecta* (C. Presl) Piper, *Flora of the Northwest Coast*. 199. 1915.
- Cerasus pattoniana* Carrière, *Revue Horticole* 135. 1872. TYPE: fig. 17.
- Cerasus glandulosus* Kellogg, *Proceedings of the California Academy of Sciences* 1: 59. 1873. TYPE: USA, [California, El Dorado Co.], Placerville, *A. Kellogg s.n.* (holotype: ? destroyed by fire at CAS). (Not *Prunus glandulosa* Thunb. in Murray, *Systema Vegetabilium*, edition 14: 463. 1784 (Bartholomew et al. 1997). Not *Cerasus glandulosa* (Thunb. ex Murray) Loisel., *Nouveau Duhamel, ou Traité des Arbres et Arbustes que l'on Cultive en France* 5: 33. 1812. Not *Prunus glandulosa* Torr. & A. Gray, *A Flora of North America* 1: 408. 1840.)
- Cerasus californica* Greene, *Flora Franciscana* 1: 50. 1891. TYPE: USA, California, Siskiyou Co., near Yreka, 6 Jun 1876, *E. L. Greene 824* (lectotype, here designated, NDG-23772!).
- Prunus corymbulosa* Rydb., *Memoirs of the New York Botanical Garden* 1: 226. 1900. TYPE: USA, Montana, Exploration of Montana and Yellowstone Park, Bridger Mountains, alt. 7000 ft, 18 Jun 1897, *P. A. Rydberg & E. A. Bessey 4437* (lectotype, here designated, NY-436475!; isolectotype: NY-436474!).
- Cerasus arida* Greene, *Proceedings of the Biological Society of Washington* 18: 57. 1905. TYPE: USA, California, San Bernardino Co., Bear Valley, San Bernardino Mountains and their eastern base, alt. 6500 feet, 25 Jun 1894, *S. B. Parish 3379* (holotype: US!).
- Cerasus crenulata* Greene, *Proceedings of the Biological Society of Washington* 18: 56. 1905. TYPE: USA, New Mexico, "Socorro Co.", Mogollon Mountains, on or near the West Fork of the Gila River, alt. 8,000 feet, 23 Aug 1903, *O. B. Metcalfe 587* (holotype: NDG?, n.v.; isotypes: GH!, US!).—*Prunus crenulata* (Greene) Tidestr., *Proceedings of the Biological Society of Washington* 40: 119. 1927.—*Prunus emarginata* (Douglas ex Hook.) Eaton var. *crenulata* (Greene) Kearney & Peebles, *Journal of the Washington Academy of Sciences* 29: 481. 1939.
- Cerasus kelloggiana* Greene, *Proceedings of the Biological Society of Washington* 18: 58. 1905. TYPE: USA, California, Placer Co., Emigrant Gap, 28 May 1882, [cited in error as 28 June 1882 in protologue, labeled 28 May 1882 by Jones on all sheets seen], *M. E. Jones 2693* (lectotype, here designated, NY-418580!, isolectotypes: A!, CAS!, DS, NY-803929!, POM!, UC(2), US?, n.v.).
- Cerasus obliqua* Greene, *Proceedings of the Biological Society of Washington* 18: 59. 1905. TYPE: USA, California, Butte Co., near Oroville, altitude 175 feet, 2 Oct 1896, *H. E. Brown 117* (holotype: US!; isotypes: NY!, RM).
- Cerasus obtusata* Greene, *Proceedings of the Biological Society of Washington* 18: 60. 1905. TYPE: USA, Oregon, [Grant Co.], Silvies-Calamity, southeastern Oregon, Aug 1901, *D. Griffiths & E. L. Morris 810* (holotype: US!). (Not *Prunus obtusata* Koehne, *Plantae Wilsonianae* 1: 66. 1911.).
- Cerasus padifolia* Greene, *Proceedings of the Biological Society of Washington* 18: 59. 1905. TYPE: USA, Nevada, Carson City, foothills, altitude 6000 feet, 2 Jun 1897, *M. E. Jones s.n.* (holotype: US!; isotype: CAS!).—*Prunus padifolia* (Greene) A. Nelson, *Botanical Gazette* 52: 265. 1911.
- Cerasus parvifolia* Greene, *Proceedings of the Biological Society of Washington* 18: 59. 1905. TYPE: USA, California, [Siskiyou Co.], S side of Mt. Shasta, Jul 1897, *H. E. Brown s.n.* (holotype: US?, n.v.).
- Cerasus prunifolia* Greene, *Proceedings of the Biological Society of Washington* 18: 57. 1905. TYPE: USA, California, Fresno Co., Dinkey Creek, alt. 8000 ft, 25 Jun-15 Jul 1900, *H. M. Hall & H. P. Chandler 385* (holotype: US!; isotype: K!).—*Prunus prunifolia* (Greene) Shaffer, *North American Trees*. 500. 1908.
- Cerasus rhamnoides* Greene, *Proceedings of the Biological Society of Washington* 18: 58. 1905. TYPE: USA, California, Amador Co., Mud Springs, elev. 5500 feet, 1893, *G. Hansen 1474* (holotype: US!; isotype: DS!). (Not *Prunus rhamnoides* Koehne, *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 52: 283. 1915.).
- Cerasus trichopetala* Greene, *Proceedings of the Biological Society of Washington* 18: 60. 1905. TYPE: USA, Montana, Columbia Falls, flower 28 May 1894, *R. S. Williams 1005* (holotype: US?, n.v.; isotypes: MONT!, MONTU!(2)).—*Prunus trichopetala* (Greene) Blank., *Montana Agricultural College Science Studies, Botany* 1: 70. 1905.

The original collections of bitter cherry, *Prunus emarginata*, were gathered by David Douglas between 1825 and 1827 in the upper Columbia River valley, above Fort Vancouver (McKelvey 1955). The epithet *emarginata* is unfortunate.

TABLE 1. REPORTED HYBRIDS INVOLVING *PRUNUS AVIUM* OR *P. EMARGINATA*.

<i>Prunus avium</i> hybrids	
<i>Prunus cerasus</i> L. = <i>Prunus avium</i> (L.) L. × <i>P. fruticosa</i> Miyoshi (Oldén and Nybom 1968; Mowrey and Werner 1990)	
<i>Prunus</i> CV 'Colt' = <i>Prunus avium</i> × <i>P. pseudocerasus</i> Lindl.	
<i>Prunus</i> × <i>fontanesiana</i> (Spach) C. K. Schneider = <i>Prunus avium</i> × <i>P. mahaleb</i> L.	
<i>Prunus</i> × <i>gondouinii</i> (Poit. & Turpin) Rehder = <i>Prunus avium</i> × <i>P. cerasus</i> (Fogle 1975; Mowrey and Werner 1990)	
<i>Prunus</i> × <i>schmittii</i> Rehder = <i>Prunus avium</i> × <i>P. canescens</i> M. Vilm. & Bois	
<i>Prunus</i> × <i>stacei</i> Wójcicki = <i>Prunus avium</i> × <i>P. cerasus</i> × <i>P. fruticosa</i>	
<i>Prunus</i> × <i>zumbra</i> Rosend. & Butters = <i>Prunus avium</i> × <i>P. pensylvanica</i> L.f. × <i>P. pumila</i> L. var. <i>besseyi</i> (L. H. Bailey) Gleason (Fogle 1975)	
<i>Prunus emarginata</i> hybrids	
<i>Prunus emarginata</i> (Douglas ex Hook.) Eaton × <i>P. pensylvanica</i> (Brayshaw 1996, p. 206; Taylor and Taylor 1981).	
<i>Prunus</i> × <i>puguetensis</i> A. L. Jacobson & Zika = <i>Prunus emarginata</i> × <i>P. avium</i>	

Hooker (1832), working with Douglas' manuscript and collections after his death, described the leaves as: "foliis ... apice obtusis saepe emarginatis," suggesting the obtuse leaf tips are often shallowly notched. After reviewing the foliage of hundreds of herbarium specimens and wild populations, we have concluded the emarginate apex is an atypical condition, and is barely visible on a few leaves of Douglas' material at Kew.

Although overlooked in modern indices and floras, it has been pointed out by Merrill and Reeder (1946) that the first to make the combination *Prunus emarginata* was Amos Eaton, in 1836. Since its description it has been split into many named variations (e.g., Greene 1905), which we do not recognize. The most commonly accepted named form is pubescent, *P. emarginata* var. *mollis* (Douglas ex Hook.) Brewer (Hitchcock and Cronquist 1961). As far as known, the hybrid *P. ×puguetensis* involves only pubescent plants. From our review of types and the literature, none of the names referred to synon-

ymy under *P. emarginata* represent the hybrid *P. ×puguetensis*.

Prunus emarginata is found from the Queen Charlotte Islands in British Columbia (c. 54° N) south to Arizona (c. 32° N) and southwestern New Mexico. It is recorded in nine states and one Canadian province (Little 1976; Welsh et al. 1987; Kartesz 2003). The range maps in Little (1976) show *Prunus emarginata* is the western counterpart or extension of *P. pensylvanica* L.f. Their ecological roles are as similar as their appearances. Moreover, where their ranges overlap in British Columbia, they are reported to hybridize (Table 1).

We provide a key to separate *Prunus* × *puguetensis* from its parents and other members of the genus in the Pacific Northwest. Taxa native, naturalized, or casually escaping from cultivation are included. The key is designed for flowering material, but for certain deciduous taxa it may help to search for the previous year's mature leaves and pits on the ground beneath the tree.

KEY TO *PRUNUS* IN BC, WA, AND OR

1. Leaves evergreen. 2
2. Inflorescence longer than leaves; petioles and inflorescence rachis dark purple; petal venation dendritic *P. lusitanica* L.
- 2'. Inflorescence shorter than leaves; petioles and inflorescence rachis green; petal venation palmate *P. laurocerasus* L.
- 1'. Leaves deciduous 3
3. Ovary pubescent. 4
4. Ovary with scattered hairs 5
5. Flowers pink, in umbels; pedicels 25–40 mm long; leaf tips cuspidate and acuminate. *P. yedoensis* Matsum.
- 5'. Flowers white, in corymbs; pedicels 5–19 mm long; leaf tips gradually acute or obtuse *P. emarginata*
- 4'. Ovary densely hairy. 6
6. Flowers on pedicels 0.5–1.0 cm long; style base glabrous; flowers white; native shrub in western and southern Oregon *P. subcordata* Benth.
- 6'. Flowers essentially sessile; style base long-hairy; flowers white or pink; trees escaped or persisting from cultivation 7
7. Axillary buds solitary; terminal winter bud absent; apex of bud scales and sepal margins essentially glabrous; leaves about as long as wide *P. armeniaca* L.
- 7'. Axillary buds in clusters of 3; terminal winter bud present; apex of bud scales and sepal margins tomentose; leaves lanceolate, much longer than wide 8
8. Flowers white (or palest pink); mature leaves 7–10 cm long, fruit the familiar almond, elliptic, dry, dehiscent, with a thick leathery skin, stone pitted. . . *P. dulcis* (Mill.) D. A. Webb

- 8'. Flowers pink; mature leaves 10–18 cm long; fruit the familiar peach, subglobose, fleshy, indehiscent, with a thin skin; stone ridged *P. persica* (L.) Batsch 9
- 3'. Ovary glabrous. 9
9. Leaves bronzy or dark purple; flowers white or pink *P. cerasifera* Ehrh. 10
- 9'. Leaves green; flowers white 10
10. Flowers solitary, sessile or on pedicels < 3 mm, anthers yellow-orange to orange-red *P. spinosa* L. 11
- 10'. Flowers usually 2 or more per node, on easily visible pedicels > 5 mm; anthers yellow 11
11. Flowers in racemes or corymbs (inflorescence with a rachis) 12
12. Flowers in short corymbs of 2–15 flowers 13
13. Some sepals erose or glandular serrate, at least towards apex. *P. emarginata* × *virginiana* 14
- 13'. All sepals entire 14
14. Petals 7–14 mm long *P. ×pugetensis* 15
- 14'. Petals 4–6 mm long 15
15. Leaves less than 1.5 × as long as wide; leaf bases cordate to nearly truncate; sepals spreading; petals elliptic or elliptic-lanceolate *P. mahaleb* L. 16
- 15'. Leaves more than 2 × as long as wide; leaf bases tapered, cuneate; sepals reflexed; petals suborbicular. 16
16. Leaf tips rounded to acute; bud scales at base of inflorescence persistent; peduncle sometimes leafy, sometimes elongate; wide-spread in and west of Rocky Mountains. *P. emarginata* 16'
- 16'. Leaf tips gradually acuminate or attenuated (well developed on oldest leafy shoots, or on last year's leaves under the plant); bud scales at base of inflorescence usually early deciduous; peduncle never leafy, often 1–2 mm long; east of Rocky Mountains, in our area restricted to SE BC *P. pennsylvanica* L. f. 17
- 12'. Flowers in long racemes of 20+ flowers 17
17. Longer petals 6–9 mm long, usually longer than wide; flowers 14–20 mm diam.; inner surface of hypanthium densely pubescent near ovary; last year's pits (look under tree) sculpted and irregularly ridged *P. padus* L. 18
- 17'. Longer petals 3–5 mm long, suborbicular; flowers 10–12 mm diam.; inner surface of hypanthium glabrous or thinly pubescent near ovary; pit surface essentially smooth 18
18. Leaves dull above, underside glabrous; calyx deciduous from developing fruit; isolated small tree, or thicket-forming shrub; common native throughout *P. virginiana* L. 19
- 18'. Leaves glossy above, underside with band of rusty pubescence along lower midvein; calyx persists at base of developing fruit; solitary tree; rare escape from cultivation in urban areas west of the Cascade Mountains *P. serotina* Ehrh. 19
- 11'. Flowers in umbels (inflorescence without a rachis) 19
19. Umbels elevated from twig on a peduncle *P. ×pugetensis* 20
- 19'. Umbels sessile on twig 20
20. Sepals smooth-margined 21
21. Flowers 23–35 mm diam.; petals 11–16 mm long, tips notched *P. avium* 21'
- 21'. Flowers 9–17 mm diam.; petals 4–7 mm long, tips blunt go to lead 16
- 20'. Sepals glandular-serrate or glandular-ciliate 22
22. Leaf tips acuminate to attenuate, marginal teeth acuminate and prominent; rare native on our eastern margin *P. americanum* Marshall 23
- 22'. Leaf tips blunt to acute, marginal teeth obtuse to acute, in most species not prominent; native in SW portion of our range, or widely scattered escapes from cultivation 23
23. Hypanthium, pedicels (and usually twigs) pubescent 24
24. Leaves glaucous below; sepals often obscured by dense pubescence, occasionally glabrous; inflorescence often densely pubescent, occasionally glabrous; leaves usually cordate or rounded at base; native in southern and western Oregon. *P. subcordata* 24'
- 24'. Leaves pale green, not strongly glaucous below; sepals lightly pubescent or glabrous; inflorescence glabrous or sparsely pubescent; leaves cuneate at base; widespread escape from cultivation throughout *P. domestica* L. 25
- 23'. Hypanthium, pedicels (and usually twigs) glabrous 25
25. Hypanthium length < width; sepals with band of hair across base on inner (adaxial) surface; underside of leaf with dense band of hair along lower midvein, otherwise essentially glabrous; flowering in March or the first week of April *P. cerasifera* 25'
- 25'. Hypanthium length ≥ width; sepals glabrous within, or uniformly hairy; underside of leaf quickly glabrous, or hairy over entire surface;

- flowering in late April or May 26
- 26. Sepals 3.2–5.0 mm long; flowering pedicels mostly > 1.5 cm long; leaves folded in bud (conduplicate), quickly glabrous beneath, coarsely serrate; leaf base cuneate; fruit the familiar sour or pie cherry; rare escape from cultivation *P. cerasus* L.
- 26'. Sepals 2.3–2.7 mm long; flowering pedicels mostly < 1 cm long; leaves rolled in bud (convolute), hairy beneath, finely serrate; leaf base rounded or subcordate; fruit a small plum; native to southern and western Oregon *P. subcordata*

ECOLOGY

Prunus × *pugetensis* has been found in thickets, field and forest margins, roadsides, in disturbed second growth conifers, and in mixed conifer and deciduous forest. Elevations range from 10 to 410 m, and sites vary from flat to gentle slopes at all aspects. Common associates include: *Acer circinatum* Pursh, *A. macrophyllum* Pursh, *Alnus rubra* Bong., *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem., *Arbutus menziesii* Pursh, *Cornus nuttallii* Audubon ex Torr. & A. Gray, *Corylus cornuta* Marshall, *Crataegus monogyna* Jacq., *Gaultheria shallon* Pursh, *Holodiscus discolor* (Pursh) Maxim., *Oemleria cerasiformis* (Torr. & A. Gray ex Hook. & Arn.) J. W. Landon, *Polystichum munitum* (Kaulf.) C. Presl, *Populus balsamifera* L., *Prunus avium*, *P. emarginata*, *P. virginiana* L., *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus garryana* Douglas ex Hook., *Rhamnus purshiana* DC., *Rosa gymnocarpa* Nutt., *Rubus armeniacus* Focke, *R. spectabilis* Pursh, *R. ursinus* Cham. & Schltldl., *Salix scouleriana* Barratt ex Hook., *Sorbus aucuparia* L., *Symphoricarpos albus* (L.) S. F. Blake, *Thuja plicata* Donn ex D. Don, *Vaccinium ovatum* Pursh, and *V. parvifolium* Sm.

Pollination and dispersal. We have noted a number of insect species visiting the flowers of *Prunus* × *pugetensis*, including the introduced honeybee (*Apis mellifera*), some *Bombus*, and ants. Flowering has been recorded from 12 April to 24 May. Fruit can ripen by the beginning of June in exceptional years, but typically matures by 15–24 July. We have not observed animals eating the fruits and dispersing the seed of *P. ×pugetensis*. Dispersal of the two parents suggests hybrid seeds are probably bird dispersed. We have seen *P. avium* fruits, similar in size to the fruits of *P. ×pugetensis*, eaten by American crows (*Corvus brachyrhynchos*), American robins (*Turdus migratorius*), Steller’s jays (*Cyanocitta stelleri*), and European starlings (*Sturnus vulgaris*) in the Pacific Northwest. In eastern Canada cultivated *P. avium* fruits are consumed by four bird species: American robins, common grackles (*Quiscalus quiscula*), Baltimore orioles (*Icterus galbula*), and European starlings (Brown 1974). The authors have observed cedar waxwings (*Bombycilla cedrorum*) and American robins swallowing *P. emarginata* fruits in western Washington. While

the hybrid cherry may be bird dispersed, it is also possible that fallen fruits and seed are moved by a number of mammals (Martin et al. 1961), including Virginia opossum (*Didelphis virginiana*) and raccoon (*Procyon lotor*).

EVIDENCE FOR HYBRID STATUS

By using a combination of leaf and inflorescence characters, we found that *Prunus* × *pugetensis* differed strongly from most wild and cultivated *Prunus* in our area. *Prunus virginiana*, for example, is indigenous and occasional in the range of *P. ×pugetensis*, but has black fruits and elongate racemes, unlike the red-fruited umbels and corymbs of *P. ×pugetensis*.

The only morphologically similar species, *P. avium* and *P. emarginata*, were also the only representatives of the genus consistently present at populations of *P. ×pugetensis*. Both *Prunus avium* and *P. emarginata* are reported to form other hybrids (Table 1). Morphological evidence places *P. ×pugetensis* intermediate between the two proposed parental species with which it grows, strongly suggesting that it is a hybrid (Table 2). Leaf shape, size, and toothing of the hybrid are intermediate, as shown in Fig. 3. Characters of the inflorescence, flowering period, fruit size, stone surface, petal shape, autumn leaf color, and winter twigs are also all intermediate, showing the influence of both *P. emarginata* and *P. avium* (Fig. 4). In general, the hybrid is too robust and large in its leaves and flowers to be called *P. emarginata*. It is too slender and pubescent to be called *P. avium* when in flower. Its blooms make a showier display than *P. emarginata*, rather like *P. avium*.

Many known hybrids have reduced fertility. In 2002, we visited wild populations of *Prunus avium*, *P. ×pugetensis*, and *P. emarginata* in King Co., Washington, counted flowers on marked branches, and revisited when green fruits were approaching maturity. *P. ×pugetensis* aborted more than 99% of its flowers (Table 2), and we had difficulty finding fruits, seeds, and seedlings to include in its formal description, despite searches over five field seasons. In sharp contrast, the fully fertile parents both produced abundant fruit (<40% abortion) and easily detected seedlings. We opened five seeds of *P. ×pugetensis*, and they were filled, but we have not run germination experiments to see if they are viable.

TABLE 2. MORPHOLOGICAL COMPARISON OF WILD *PRUNUS AVIUM*, *P. ×PUGETENSIS*, AND *P. EMARGINATA* FROM WEST OF THE CASCADES MOUNTAINS IN WASHINGTON AND BRITISH COLUMBIA.

	<i>P. avium</i>	<i>P. ×pugetensis</i>	<i>P. emarginata</i>
Mid-summer leaves			
Shape	Obovate	elliptic-obovate	Elliptic
Marginal teeth/cm	3–7, spread	6–11, ascend	10–21, incurved
Tooth height (mm)	0.3–3.6	0.1–1.1	0.1–0.3
Apex	cuspidate, acuminate	gradually acute	gradually acute or blunt
Length × width (cm)	7–17.5 × 4–8	4–15 × 2–6	2–7.5 × 1–3.5
Mature leaf hairs	± glabrous	mostly pubescent	pubescent
Twigs			
Pubescence	Glabrous	mostly hairy	mostly hairy
Bundle scars	Spaced	usually spaced	usually clustered
Inflorescence			
Inflorescence types	sessile umbel	umbel, peduncled umbel, or corymb	corymb
Leafy peduncle	Never	occasional	occasional
Flowers/inflorescence	2–5	2–9	5–14
Pedicels (mm)	17–64	5–35	5–19
Flowers (shaded plants have the smaller dimensions)			
Diameter (mm)	23–35	13–28	9–17
% early aborted in 2002 (<i>n</i> = number of flowers)	38 (<i>n</i> = 429)	99.3 (<i>n</i> = 990)	21 (<i>n</i> = 771)
Petal pubescence	Glabrous	usually hairy	usually hairy
Petal apex	deep notch	blunt or slightly notched	blunt
Hypanthium	Glabrous	hairy	usually hairy
Ovary	Glabrous	glabrous	glabrous or slightly hairy
Fruits (shaded plants have the smaller dimensions)			
Diameter (mm)	11–21	10–19	7–12
Color	yellow, red, or black	yellow or red	red
Pit (stone, endocarp)			
Shape	subglobose, ellip.-globose	elliptic-globose	ellipsoid
Surface	Smooth	slightly roughened	roughened
Raised lateral veins	Absent	2–4, straight, unforked, short	2–4, curved, forked, elongate
Pit length × width (mm)	9–12 × 7–9	7–11 × 4–8	6–10 × 4–6

Other hybrids between native and introduced species. In our area, there are few records of native species hybridizing with exotics, and such crosses are generally uncommon to rare in the field. Rosaceous examples we have seen include native *Malus fusca* (Raf.) C. K. Schneid. crossing with *M. domestica* Borkh., producing *M. ×dawsoniana* Rehder in the Puget Trough (Dickson et al. 1991; Zika 2004). Love and Feigin (1978) discovered introduced *Crataegus monogyna* hybridizing with native *C. suksdorfii* (Sarg.) Kruschke in the wet prairie remnants of the Willamette Valley of Oregon. *Crataegus monogyna* was also found crossing with native *C. punctata* Jacq. in Ontario (Wells and Phipps 1989). In Kitsap Co., Washington, the authors found one clone of *Rosa nutkana* C. Presl × *R. rugosa* Thunb. (Zika 14908 & Jacobson WTU). In Québec introduced *Geum urbanum* hybridizes with two native taxa (Bernard and Gauthier 1986).

Outside the Rosaceae, there are a few spontaneous crosses between native North American

taxa and exotics, such as in *Impatiens* (Ornduff 1967), *Juglans* (Sargent 1922), *Lupinus* (Wear 1998), *Populus* (Barnes 1961; Spies and Barnes 1982), *Quercus* (Palmer 1948; Hardin 1975), *Schoenoplectus* (Smith 2002), *Spartina* (Anttila et al. 1998), and *Typha* (Smith 2000).

It is likely that there are other hybrids overlooked in our area, when widespread and abundant ones in *Polygonum* (Zika and Jacobson 2003) and *Tamarix* (Gaskin and Schaal 2002; Gaskin and Shafroth 2005) were only recently detected. There is concern about the invasive nature of some hybrids, which are degrading natural areas in the United States (Ellstrand and Schierenbeck 2000), or threatening rare native taxa via introgression (Levin et al. 1996; Rhymer and Simberloff 1996; Vilà et al. 2000). We do not feel that *Prunus ×pugetensis* represents a threat to native plant communities in our area. The native parent is common; the hybrid produces insignificant fruit crops (Table 2). We have not observed hybrid seedlings, so we believe *P. ×pugetensis* is

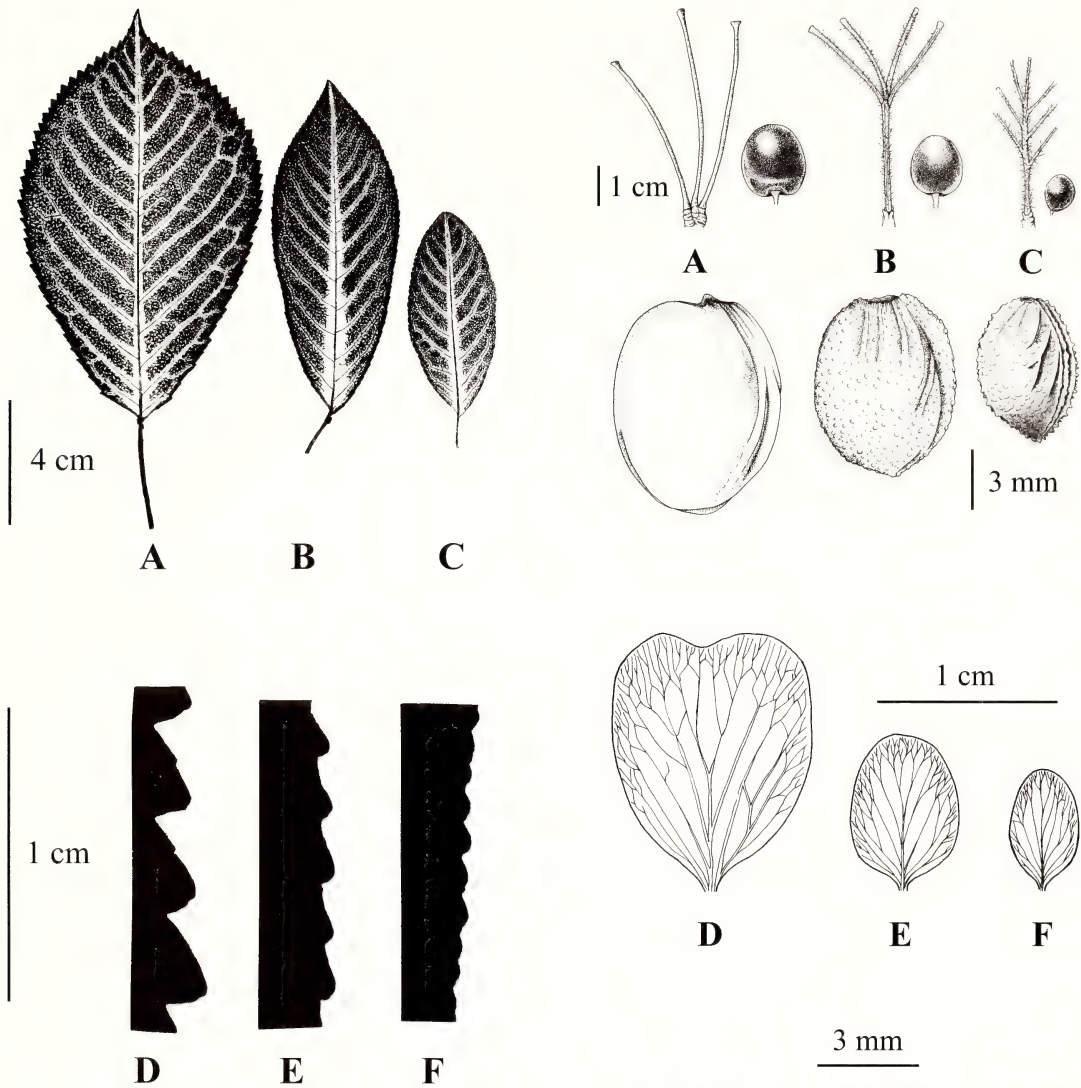


FIG. 3. Comparison of *Prunus* × *pugetensis* with parents. *Prunus avium* on left, *P. ×pugetensis* in center, *P. emarginata* on right. A–C) Leaf shape and size. D–E) Leaf margins.

unlikely to spread aggressively. Each hybrid colony we have found appears to represent essentially sterile spontaneous hybrids, produced locally by crossing of the parental species. Nonetheless, there may be some economic value to the hybrid as an ornamental street tree, with its showy flowers, sturdy growth in urban settings, and lack of fruit. By comparison, the widespread introduction *P. avium* is a much more problematic species in natural areas, with its abundant fruit crop and plentiful reproduction by seed.

ACKNOWLEDGMENTS

We thank the curators and staff of the following institutions for access to specimens or loans: A, CAS, COCO, DAO, DBG, DS, ELRG, FHL, FTU, GH, K,

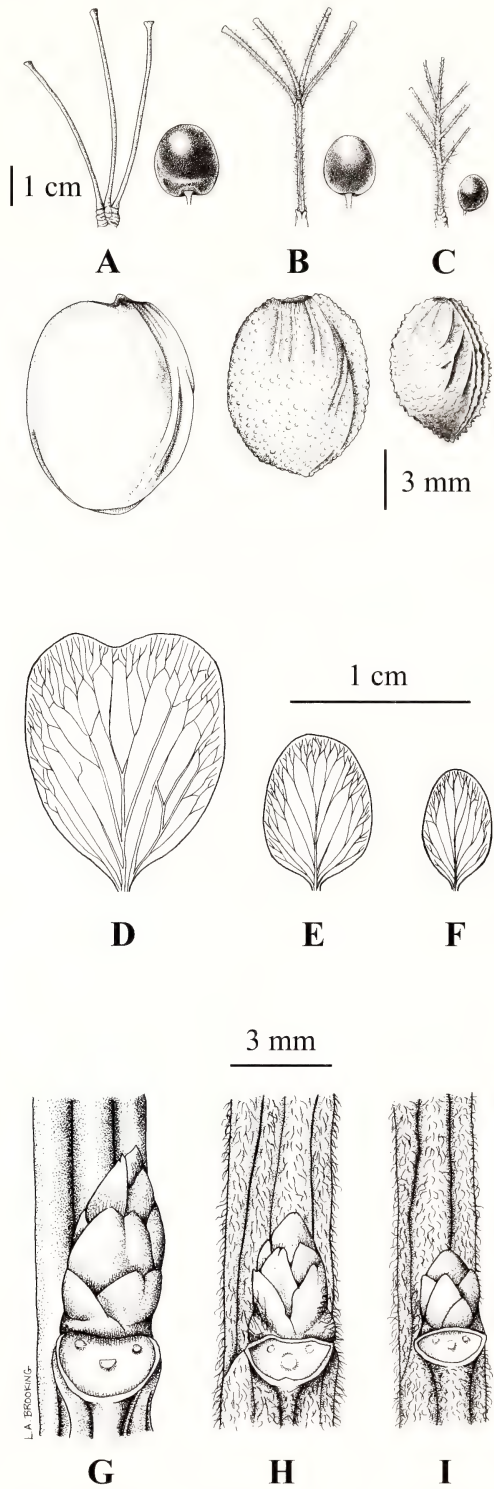


FIG. 4. Comparison of *Prunus* × *pugetensis* with parents. *Prunus avium* on left, *P. ×pugetensis* in center, *P. emarginata* on right. A–C) Inflorescence types, fruit sizes, endocarp surface and size. D–F) Petals. G–I) Winter twigs and buds, leaf scars, vascular bundle scars.

KHD, MICH, MONT, MONTU, NDG, NY, ORE, OSC, POM, PR, PRC, RSA, SD, SOS, SPC, UBC, US, WILLU, WTU, WTUH, WWB, as well as collections not included in Index Herbariorum (Holmgren et al. 1990): The Evergreen State College, Olympia ("evsc"); Olympic National Forest, Olympia; Olympic National Park, Port Angeles; University of Puget Sound, Tacoma; Pacific Lutheran University, Tacoma; and Reed College, Portland, Oregon. We are grateful to Jan Kirschner and Jan Štěpánek for searching for Haenke collections, to Ken Chambers for correcting the Latin diagnosis, to Ben Legler for preparing the map, to Linda Brooking for Figs. 1 and 4, and to our reviewers for improving the manuscript. Dorothy Naas and Mildred Arnot kindly provided assistance in relocating their station for the hybrid in the San Juan Islands.

LITERATURE CITED

- ANTTILA, C. K., C. C. DAEHLER, N. E. RANK, AND D. R. STRONG. 1998. Greater male fitness of a rare invader (*Spartina alterniflora*, Poaceae) threatens a common native (*Spartina foliosa*) with hybridization. *American Journal of Botany* 85:1597–1601.
- BARNES, B. V. 1961. Hybrid aspens in the lower peninsula of Michigan. *Rhodora* 63:311–324.
- BARTHOLOMEW, B., D. H. NICOLSON, AND B. NORDENSTAM. 1997. Author citation of Thunberg's new species in Murray's *Systema vegetabilium*, ed. 14. *Taxon* 46:311–314.
- BERNARD, J. P. AND R. GAUTHIER. 1986. Observations sur le *Geum urbanum* L. dans la région de Québec et description de deux hybrides. *Le Naturaliste Canadien* 113:317–324.
- BORTIRI, E., S. H. OH, J. JIANG, S. BAGGETT, A. GRANGER, C. WEEKS, M. BUCKINGHAM, D. POTTER, AND D. E. PARFITT. 2001. Phylogeny and systematics of *Prunus* (Rosaceae) as determined by sequence analysis of ITS and the chloroplast *trnL-trnF* spacer DNA. *Systematic Botany* 26:797–807.
- BRAYSHAW, T. C. 1996. *Trees and Shrubs of British Columbia*. University of British Columbia Press, Vancouver, BC.
- BROWICZ, K. AND D. ZOHARY. 1996. The genus *Amygdalus* L. (Rosaceae): Species relationships, distribution and evolution under domestication. *Genetic Resources and Crop Evolution* 43:229–247.
- BROWN, R. G. B. 1974. Bird damage to fruit crops in the Niagara Peninsula. Canadian Wildlife Service Report Series, No. 27, Environment Canada Wildlife Service, Ottawa, ON.
- DICKSON, E. E., S. KRESOVICH, AND N. F. WEEDEN. 1991. Isozymes in North American *Malus* (Rosaceae): hybridization and species differentiation. *Systematic Botany* 16:363–375.
- ELLSTRAND, N. C. AND K. A. SCHIERENBECK. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Pp. 289–309 in F. J. Ayala, W. M. Fitch, and M. T. Clegg (eds.), *Variation and Evolution in Plants and Microorganisms: Towards a New Synthesis 50 Years after Stebbins*. National Academy Press, Washington, DC.
- ENDO, Y. 2001. *Prunus* L. Pp. 128 in K. Iwatsuki, D. E. Boufford, and H. Ohba (eds.), *Flora of Japan*, Volume IIb, Angiospermae Dicotyledoneae Archichlamydeae (b). Kodansha Ltd., Tokyo, Japan.
- FOGLE, H. W. 1975. Cherries. Pp. 348–366 in J. Janick and J. N. Moore (eds.), *Advances in Fruit Breeding*. Purdue University Press, West Lafayette, IN.
- GASKIN, J. F. AND B. A. SCHAAL. 2002. Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. *Proceedings of the National Academy of Sciences of the United States of America* 99:11256–11259.
- AND P. B. SHAFROTH. 2005. Hybridization of *Tamarix ramosissima* and *T. chinensis* (saltcedars) with *T. aphylla* (athel) (Tamaricaceae) in the southwestern USA determined from DNA sequence data. *Madroño* 52:1–10.
- GREENE, E. L. 1905. Some west American red cherries. *Proceedings of the Biological Society of Washington* 18:55–60.
- GREUTER, W., J. MCNEILL, F. R. BARRIE, H. M. BURDET, V. DEMOULIN, T. S. FILGUEIRAS, D. H. NICOLSON, P. C. SILVA, J. E. SKOG, P. TREHANE, N. J. TURLAND, AND D. L. HAWKSWORTH. 2000. *International Code of Botanical Nomenclature* (St. Louis Code). Koeltz Scientific Books, Königstein, Germany.
- HARDIN, J. W. 1975. Hybridization and introgression in *Quercus alba*. *Journal of the Arnold Arboretum* 56:336–363.
- HITCHCOCK, C. L. AND A. CRONQUIST. 1961. *Vascular Plants of the Pacific Northwest; Part 3: Saxifragaceae to Ericaceae*. University of Washington Press, Seattle, WA.
- HOLMGREN, P., N. H. HOLMGREN, AND L. C. BARNETT. 1990. *Index Herbariorum*. Part 1: The Herbaria of the World. Eighth Edition. New York Botanical Garden, Bronx, NY.
- HOOKE, W. J. 1832. *Flora Boreali-Americana*, Volume 1. Henry G. Bohn, London.
- HULTÉN, E. 1968. *Flora of Alaska and Neighboring Territories*. Stanford University Press, Stanford, CA.
- HUXLEY, A., M. GRIFFITHS, AND M. LEVY (eds.). 1992. *The New Royal Horticulture Society Dictionary of Gardening*. Volume 3, L to Q. The MacMillan Press Limited, London, UK.
- KARTESZ, J. T. 2003. A Synonymized Checklist and Atlas with Biological Attributes for the Vascular Flora of the United States, Canada, and Greenland. Second Edition. In J. T. Kartesz and C. A. Meacham (eds.), *Synthesis of the North American flora*, CD-ROM Version 2.0. J. T. Kartesz & Phylosystems Corporation, Chapel Hill, NC.
- KU, T. C. AND B. BARTHOLOMEW. 2003a. *Prunus* Linnaeus. *Flora of China* 9:401–403.
- AND ———. 2003b. *Padus* Miller. *Flora of China* 9:420–426.
- LEE, S. AND J. WEN. 2001. A phylogenetic analysis of *Prunus* and the Amygdaloideae (Rosaceae) using ITS sequences of nuclear ribosomal DNA. *American Journal of Botany* 88:150–160.
- LEVIN, D. A., J. FRANCISCO-ORTEGA, AND R. K. JANSEN. 1996. Hybridization and the extinction of rare plants. *Conservation Biology* 10:10–16.
- LI, C. L. AND B. BARTHOLOMEW. 2003. *Cerasus* Miller. *Flora of China* 9:404–420.
- LITTLE, E. L. 1976. *Atlas of United States Trees*, Volume 3: Minor Western Hardwoods. United States Department of Agriculture, Forest Service, Miscellaneous Publication No. 1314, United States Government Printing Office, Washington, DC.

LOVE, R. AND M. FEIGEN. 1978. Interspecific hybridization between native and naturalized *Crataegus* (Rosaceae) in western Oregon. *Madroño* 25:211–217.

LU, L. T. AND B. BARTHOLOMEW. 2003. *Laurocerasus* Duhamel. *Flora of China* 9:426–430.

——, T. C. KU, C. L. LI, C. ALEXANDER, B. BARTHOLOMEW, A. R. BRACH, D. E. BOUFFORD, H. IKEDA, H. OHBA, K. R. ROBERTSON, AND S. A. SPONGBERG. 2003. Rosaceae. *Flora of China* 9:46–434.

MABBERLEY, D. J. 1997. *The Plant-Book: A Portable Dictionary of the Vascular Plants*, 2nd ed. Cambridge University Press, Cambridge, UK.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1961 reprint. *American Wildlife & Plants: A Guide to Wildlife Food Habits*. Dover Publications, Inc., New York, NY.

MCKELVEY, S. D. 1955. Botanical Exploration of the Trans-Mississippi West 1790–1850. The Arnold Arboretum of Harvard University, Jamaica Plain, MA.

MCVAUGH, R. 1951. A revision of the North American black cherries (*Prunus serotina* Ehrh., and relatives). *Brittonia* 7:279–315.

MERRILL, E. D. AND J. R. REEDER. 1946. New plant names published by Amos Eaton between the years 1817 and 1840. *Bartonia* 24:26–79.

MONTGOMERY, L., M. KHALAF, J. P. BAILEY, AND R. J. GORNALL. 1997. Contributions to a cytological catalogue of the British and Irish flora. *Watsonia* 21:365–368.

MOWREY, B. D. AND D. J. WERNER. 1990. Phylogenetic relationships among species of *Prunus* as inferred by isozyme markers. *Theoretical and Applied Genetics* 80:129–133.

OHBA, H. AND Y. ENDO. 2001. *Cerasus* Mill. Pp. 128–144 in K. Iwatsuki, D. E. Boufford, and H. Ohba (eds.), *Flora of Japan*, Volume IIb, Angiospermae Dichotyledoneae Archichlamydeae (b). Kodansha Ltd., Tokyo, Japan.

OLDÉN, E. J. AND N. NYBOM. 1968. On the origin of *Prunus cerasus* L. *Hereditas* 59:327–345.

ORNDUFF, R. 1967. Hybridization and regional variation in Pacific Northwestern *Impatiens* (Balsaminaceae). *Brittonia* 19:122–128.

PALMER, E. J. 1948. Hybrid oaks of North America. *Journal of the Arnold Arboretum* 29:1–48.

REHDER, A. 1940. *Manual of Cultivated Trees and Shrubs*, 2nd ed. The Macmillan Co., New York, NY.

RHYMER, J. M. AND D. SIMBERLOFF. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* 27:83–109.

ROHRER, J. R., R. AHMAD, S. M. SOUTHWICK, AND D. POTTER. 2004. Microsatellite analysis of relationships among North American plums (*Prunus* sect. *Prunocerasus*, Rosaceae). *Plant Systematics and Evolution* 244:69–75.

SARGENT, C. S. 1922. *Manual of the Trees of North America (Exclusive of Mexico)*. Houghton Mifflin Co., Boston, MA.

SAVAGE, S. 1945. *A Catalogue of the Linnaean Herbarium*. Linnean Society of London, London, UK.

SKOCDOPOLOVÁ, B. AND J. ŠTĚPÁNEK. 2002. Fate of Tadeáš Haenke's botanical collections. *Botanical Electronic News* 288, 13 May 2002. Available at: <http://www.ou.edu/cas/botany-micro/ben/ben288.html>; accessed 16 October 2006.

SMITH, S. G. 2000. Typhaceae. Pp. 278–285 in *Flora of North America Editorial Committee* (eds.), *Flora of North America North of Mexico*, Vol. 22. Magnoliophyta: Alismatidae, Arecidae, Commelinidae (in part), and Zingiberidae. Oxford University Press, New York, NY.

——. 2002. *Schoenoplectus*. Pp. 44–66 in *Flora of North America Editorial Committee* (eds.), *Flora of North America North of Mexico*, Vol. 23. Magnoliophyta: Commelinidae (in part): Cyperaceae. Oxford University Press, New York, NY.

SPIES, T. A. AND B. V. BARNES. 1982. Natural hybridization between *Populus alba* L. and the native aspens in southeastern Michigan. *Canadian Journal of Forest Research* 12:653–660.

TAYLOR, R. L. AND S. TAYLOR. 1981. *Prunus emarginata* in British Columbia. *Davidsonia* 12:78–83.

VIERECK, L. A. AND E. L. LITTLE. 1972. *Alaska Trees and Shrubs*. Agriculture Handbook No. 410, U. S. Department of Agriculture, Forest Service, Washington, DC.

VILÀ, M., E. WEBER, AND C. M. D'ANTONIO. 2000. Conservation implications of invasion by plant hybridization. *Biological Invasions* 2:207–217.

WEAR, K. S. 1998. Hybridization between native and introduced *Lupinus* in Humboldt County. M.S. thesis. Humboldt State University, Arcata, CA.

WELLS, T. C. AND J. B. PHIPPS. 1989. Studies in *Crataegus* (Rosaceae: Maloideae). XX. Interserial hybridization between *Crataegus monogyna* (series *Oxycanthae*) and *Crataegus punctata* (series *Punctatae*) in southern Ontario. *Canadian Journal of Botany* 67:2465–2472.

WELSH, S. L., N. D. ATWOOD, S. GOODRICH, AND L. C. HIGGINS (eds.). 1987. *A Utah Flora*. Great Basin Naturalist Memoirs 9, Brigham Young Univ., Provo, UT.

ZIKA, P. F. 2004. Noteworthy collections from Oregon and Washington. *Madroño* 51:395–397.

—— AND A. L. JACOBSON. 2003. An overlooked hybrid Japanese knotweed (*Polygonum cuspidatum* × *sachalinense*; Polygonaceae) in North America. *Rhodora* 105:143–152.